

Numerous independent gains of daily torpor and hibernation across endotherms, linked with adaptation to diverse environments

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Abstract

- Many endotherms from diverse taxonomic groups can respond to environmental changes through torpor, that is, by greatly reducing their energy expenditure for up to 24 hours (daily torpor) or longer (hibernation). We currently have a poor understanding of how torpor evolved across endotherms and its associations with physiological traits and ecological factors.
- To fill this gap, we thoroughly examine the evolutionary patterns of torpor and its links with 21 key physiological and ecological variables across 1338 extant endotherms.
- We find that daily torpor and hibernation are parts of an evolutionary torpor continuum, and that there are several, albeit weak, associations between torpor and species' physiological or environmental characteristics. Furthermore, we show that early endotherm ancestors likely did not hibernate and that this trait evolved multiple times in independent lineages.
- Overall, our results suggest that the remarkable variation in torpor patterns across extant endotherms cannot solely be attributed to environmental niches, but partly arises from independent gains of daily torpor and hibernation in various clades.

KEY WORDS

birds, dormancy, endotherms, evolution, hibernation, mammals, torpor

1 | INTRODUCTION

Whole-body endotherms (mammals and birds) are able to maintain their body temperature at a high and relatively constant value across a wide range of ambient temperatures by means of a much higher resting metabolic rate than that of ectotherms (Grigg et al., 2022). The energy expenditure of a normothermic resting endotherm is at its lowest and constant over a range of temperatures called the

thermoneutral zone, but many endotherm species live outside of that range and, therefore, spend significant amounts of energy (and water) on thermoregulation (Clarke, 2017; Geiser, 2021). Elevated energy costs can be unsustainable under challenging environmental conditions, such as extreme temperatures, or food or water shortages. In response to such challenges, numerous mammals and birds undergo torpor, which involves programmed and reversible decreases in metabolic rate and a corresponding drop in body

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temperature (Geiser, 2021; Nowack et al., 2020; Ruf & Geiser, 2015). Torpor patterns of endotherms can be broadly classified based on their duration as either (a) daily torpor or (b) prolonged torpor or hibernation. The former consists of torpor bouts lasting less than 24 h, whereas the latter can last from a day up to a year, albeit typically interrupted by brief rewarming periods (Geiser, 2021; Nowack et al., 2020). Differentiating between prolonged torpor (*multi-day torpor bouts sensu* Dausmann, 2014) and hibernation is less straightforward (e.g. see Nowack et al., 2020), and we henceforth refer to torpor patterns that last for more than 24 h as hibernation for the sake of brevity. Another key difference between daily torpor and hibernation is that the former results in less pronounced decreases in body temperature and metabolic rate than the latter (Geiser, 2021). It is worth noting that some species also use torpor for other purposes besides energy or water conservation, such as for predator avoidance or for coexistence with competitors (e.g. see Bieber & Ruf, 2009; Levy et al., 2011; Powers, 2004). Other forms of heterothermy, such as non-torpid heterothermy (Levesque et al., 2023) or facultative hyperthermia (*sensu* Gerson et al., 2019) have recently been recognized, but there has yet to be a systematic evaluation of both how common these are and if they correlate with the capacity to use daily torpor or hibernation.

In mammals, daily torpor and hibernation have been observed in most major taxonomic groups and torpor-capable species can be found among placentals, marsupials and monotremes (Geiser, 2021; Lovegrove, 2012; Nowack et al., 2020; Ruf & Geiser, 2015). In contrast, many orders of birds include species that are capable of daily torpor (e.g. Apodiformes, Passeriformes, Columbiformes and Strigiformes), but only a single bird species—the common poorwill (*Phalaenoptilus nuttallii*)—is known to hibernate (Geiser, 2021; McKechnie et al., 2023; McNab, 2009; Ruf & Geiser, 2015; Woods et al., 2019). Hence, torpor, as a key survival strategy, is phylogenetically widespread but scattered in mammals and birds.

There remain a number of unanswered questions as to how torpor in endotherms evolved. First, there is considerable debate as to whether daily torpor and hibernation are discrete types of torpor or parts of an evolutionary continuum without clearly distinguishable borders. On the one hand, the discrete states hypothesis is supported by the distributions of most torpor variables (e.g. minimum metabolic rate during torpor), which tend to be bimodal, with few species occupying the intermediate space (Ruf & Geiser, 2015). On the other hand, the evolutionary torpor continuum hypothesis is supported by the existence of species in these intermediate spaces, the difficulty in classifying some species (see Geiser & Mzilikazi, 2011) and the proposed evolution of homeothermy from an ancestral heterothermic state (Grigg et al., 2004; Lovegrove, 2012). From an evolutionary standpoint, these two hypotheses can be differentiated by examining the evolutionary transition rates among hibernation, daily torpor and lack of torpor (Figure 1). If the evolutionary continuum hypothesis holds, and there is no hard evolutionary boundary between daily torpor and hibernation, we would expect to observe

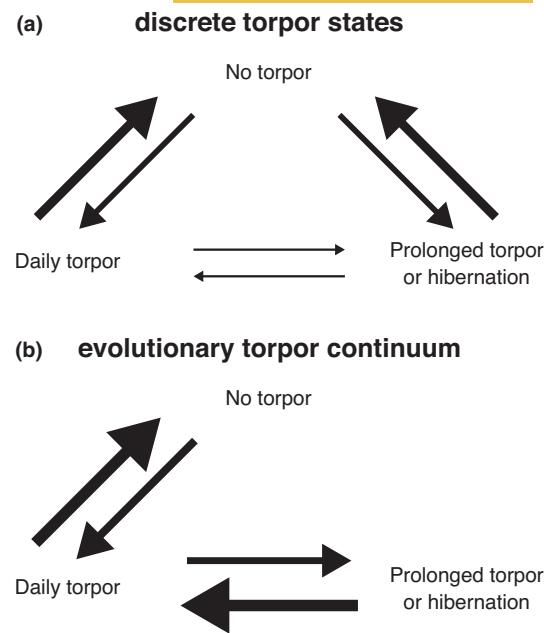


FIGURE 1 Two alternative hypotheses for the evolutionary transitions among torpor states in endotherms. Large arrows represent high transition rates, and vice versa. The two hypotheses can be differentiated based on the strength of transitions (i) between daily torpor and hibernation, and (ii) between no torpor and hibernation. The discrete torpor states hypothesis (a) posits that daily torpor and hibernation are evolutionarily distinct states and, therefore, evolutionary transitions between them should be rare. According to this hypothesis, both daily torpor and hibernation can also independently evolve from a 'no torpor' state. In contrast, the evolutionary torpor continuum hypothesis (b) posits that there is no hard boundary between daily torpor and hibernation, and hence, evolutionary transitions between them should occur frequently. Under the evolutionary torpor continuum hypothesis, direct shifts between 'no torpor' and hibernation should not occur.

high evolutionary transition rates among daily torpor and hibernation (Figure 1b). These rates would instead be much lower if daily torpor and hibernation are discrete torpor states (Figure 1a), given that evolutionary shifts between them would be much more challenging to occur. Additionally, the discrete states hypothesis allows for the possibility that daily torpor and hibernation may have evolved independently from a common ancestral state (Figure 1a).

Second, we also have an incomplete understanding of the physiological and ecological drivers that underlie evolutionary shifts in torpor. More precisely, it is not known whether, across all endotherms, the ability to enter torpor is strongly associated with specific ecophysiological variables (e.g. body mass, diet and ambient temperature seasonality), or whether such associations are weak and clade-dependent. If the former is true, it should be possible to predict—to an extent—the propensity for torpor of species for which such information is currently lacking, based on their physiology and ecological strategies. Identifying strong links between torpor and ecophysiological variables

would also shed light on the costs and benefits of daily torpor and hibernation in different environments, allowing us to more accurately forecast the impacts of global environmental change on species' populations. Furthermore, characterizing the associations between torpor and ecophysiological variables is useful for differentiating between the discrete states hypothesis and the evolutionary continuum hypothesis. If the discrete states hypothesis holds, daily heterotherms and hibernators should form distinct and well-separated peaks in the ecophysiological parameter space. Conversely, the absence of clear separation between these two groups would be consistent with the evolutionary continuum hypothesis.

Third, the origins of hibernation remain under debate. In particular, it has been argued that because of the complex physiological underpinnings of hibernation and because hibernation has been observed in monotremes, marsupials and placentals, their last common ancestor should have been capable of hibernation, with this trait later being lost in many lineages (e.g. see Geiser, 1998; Grigg et al., 2004; Malan, 1996). Furthermore, it has been hypothesized that months-long hibernation may have been key for the survival of mammals after the asteroid impact at the Cretaceous–Palaeogene boundary (e.g. Geiser et al., 2017; Lovegrove et al., 2014; Nowack et al., 2017), which radically restructured ecosystems on a global scale, causing global cooling, wildfires, acid rain, and, ultimately, a mass extinction, including of non-avian dinosaurs (Carvalho et al., 2021; Chiarenza et al., 2020; Gulick et al., 2019; Maruoka, 2019). The alternative hypothesis would be that the last common ancestors of monotremes, marsupials and placental mammals were not capable of hibernation, with this trait emerging independently in multiple clades at various time points, even after the Cretaceous–Palaeogene boundary. If this hypothesis holds, several mammalian lineages would have survived that mass extinction event without relying on hibernation. Nevertheless, smaller-scale energy conservation during the Cretaceous–Palaeogene boundary could have been achieved through daily torpor or non-torpid heterothermy, which is also characterized by flexibility in body temperature, but less pronounced than that of daily heterotherms or hibernators (Grigg et al., 2004; Grigg & Beard, 2000; Levesque et al., 2023; Lovegrove, 2012). In terms of the evolutionary torpor continuum (Figure 1b), non-torpid heterothermy would lie between no torpor and daily torpor.

To fill the aforementioned knowledge gaps, we compiled the largest dataset of torpor capabilities to date, covering 1338 extant mammals and birds, along with 21 physiological and ecological variables potentially associated with torpor. We then performed a thorough phylogenetic comparative analysis to address three key questions:

1. Are daily torpor and hibernation evolutionarily discrete torpor states or parts of a continuum?
2. Are there strong associations between torpor and key ecophysiological variables?
3. Were the early ancestors of modern mammals and birds capable of hibernation or did this trait evolve multiple times in different clades?

2 | METHODS

2.1 | Replication statement

Scale of inference	Scale at which the factor is applied	Number of replicates at the appropriate scale
Species (Mammalia and Aves)	Species	1338
Species (Mammalia)	Species	737
Species (Aves)	Species	601
Torpor-capable species (Mammalia and Aves)	Species	415

2.2 | Data analysed in the present study

To address our three key questions, we compiled a comprehensive dataset of torpor use in extant mammals and birds by combining multiple previously published datasets (Geiser, 2020, 2021; McNab, 2008, 2009; Nowack et al., 2020, 2023; Revelo Hernández et al., 2023; Ruf & Geiser, 2015). In these datasets, species were classified as belonging to one of three groups, namely (i) no torpor, (ii) daily torpor or (iii) hibernation. From these, we built a torpor dataset of 737 mammalian and 601 avian species, representing 52 orders according to the NCBI Taxonomy database (Schoch et al., 2020). We adopted the classifications used in the published datasets, following the framework employed in Ruf and Geiser (2015). More specifically, we treated species capable of both daily torpor and hibernation as hibernators to reflect the longest torpor duration exhibited by each species.

We additionally collated a dataset of 21 ecophysiological variables for each species, based on literature information where possible: (1) body mass; (2) basal metabolic rate; (3) brain mass; (4) maximum longevity; (5) migration; (6, 7) carnivory (including insectivory) and herbivory; (8) fossoriality; (9–12) diurnality, crepuscularity, nocturnality and cathemerality; (13) aquatic affinity; (14) range size; (15, 16) absolute latitude and hemisphere of the centre of the species range; and (17–21) mean temperature, temperature seasonality, annual precipitation, precipitation seasonality and net primary productivity at the centre of the range. Besides extant species, we queried palaeobiological studies to collect additional data for some of our ecophysiological variables for a few early endotherm ancestors (Supplementary Section S2.2). Descriptions and units for each variable are available in Supplementary Section S2, whereas a list of data sources—other than those already cited—is provided in the Data Sources section.

To examine the extent to which seasonal and non-seasonal environments were represented in our datasets, we used the absolute latitude at the centre of the range (where known) to classify species into (a) tropical (0–23.5°), (b) subtropical (23.5–40°), (c) temperate (40–60°) or (d) polar (60–90°). Out of all species with available

geographical coordinates, 43.9% were tropical, 26.3% subtropical, 26.2% temperate and 3.6% polar.

2.3 | Estimation of a time-calibrated phylogeny

To obtain a phylogeny of the species in our datasets, we combined the time-calibrated mammalian phylogeny of Álvarez-Carretero et al. (2022) and the non-time-calibrated avian phylogeny of Brown et al. (2017). For species in our datasets that were not included in these phylogenies, we checked whether they were present under a different name. If this was not the case, we manually added these species based on topological information from the Open Tree of Life (Hinchliff et al., 2015). We then removed species that were present in the original phylogenies but not in our datasets. The resulting tree was time-calibrated through ‘congruification’ (Eastman et al., 2013), which is implemented in the geiger R package (v. 2.0.10; Pennell et al., 2014). This approach involves identifying nodes in our tree that are compatible with those of time-calibrated reference trees, and transferring age information from the latter to the former. The remaining nodes are calibrated based on penalized likelihood with treePL (Smith & O’Meara, 2012). As reference trees, we used the Álvarez-Carretero et al. (2022) mammalian phylogeny and the phylogeny of the TimeTree database (Kumar et al., 2022).

2.4 | Phylogenetic comparative analyses

2.4.1 | Reconstructing the evolutionary pattern of torpor shifts

To examine how shifts in torpor use occur across the phylogeny, we used variants of the Mk model, a popular model of discrete trait evolution that has been applied to a wide range of traits (e.g. diet in liolemid lizards; Ocampo et al. (2022), aestivation in turtles; Macip-Ríos et al. (2023)), as well as to combinations of multiple traits and environmental variables (Cornwallis et al., 2017; Ibáñez et al., 2021). For the present study, we fitted 12 alternative Mk models (Lewis, 2001) using the phytools R package (v. 1.8–4; Revell, 2012) that differ in the following three features. First, half of these models allowed evolutionary transitions to occur between any two torpor states (in line with the discrete torpor states hypothesis; Figure 1a), whereas, in the remaining half, direct transitions between no torpor and hibernation were not allowed (in line with the evolutionary torpor continuum hypothesis; Figure 1b). Second, models differed in their patterns of transition rates between pairs of torpor states, assuming (a) a common rate for all possible transitions or (b) a common rate for forward and backward transitions (e.g. daily torpor to hibernation and hibernation to daily torpor) or (c) a different rate for each possible transition. Third, for half of the models, we simultaneously estimated both the transition rate(s) and the value of Pagel’s λ (Pagel, 1999). This allowed us to account for the possibility that torpor may not

exhibit a strong phylogenetic signal, that is, closely related species may not necessarily be considerably more similar in their torpor capabilities than randomly selected species. After obtaining all model fits, we calculated the Akaike weight (Akaike, 1974) for each candidate model and performed model averaging to obtain the final transition rates.

2.4.2 | Estimation of associations between torpor and ecophysiological variables

To investigate the links among torpor and key physiological and ecological factors, we fitted a multi-response generalized linear mixed model using the MCMCglmm R package (v. 2.34; Hadfield, 2010, 2015). This model had 22 response variables, corresponding to torpor and our 21 ecophysiological variables described earlier. Thus, the model simultaneously predicted all response variables along with their variance–covariance matrix, enabling us to estimate pairwise correlations among responses. In such a model, each response variable needs to conform to one of the distributions implemented in MCMCglmm (e.g. Gaussian, Poisson). To this end, we transformed continuous variables towards approximate normality when that was necessary. More precisely, we applied (i) a natural logarithm transformation to body mass, basal metabolic rate, brain mass, maximum longevity and annual precipitation, (ii) a square root transformation to absolute latitude and temperature seasonality, (iii) a cube root transformation to net primary productivity, (iv) a fourth root transformation to precipitation seasonality and (v) a fifth root transformation to range size.

We modelled categorical variables as threshold variables. The threshold model originates from the field of quantitative genetics (Wright, 1934) and was later applied in a phylogenetic comparative context by Felsenstein (2005). It assumes that a categorical variable is governed by an underlying unobserved continuous trait called the ‘liability’, and that shifts from one state to another occur when the liability moves past a particular threshold value. The threshold model can accommodate both binary and multistate categorical variables, provided that the states follow a particular order (e.g. we coded torpor as three ordered states of no torpor, daily torpor and hibernation). In the latter case, the model will also identify the location of the additional threshold(s) in liability space. We, therefore, applied the threshold approach—as implemented in MCMCglmm—to torpor use and all other categorical variables in our dataset, ordering their states as shown in Table S1.

In addition to data for extant species, we were able to include data for ancestral nodes (Supplementary Section S2.2) in the model. A special case was the last common ancestor of Amniota, which includes mammals and birds. Its habitat was likely coal swamps (Clack, 2012), suggesting either moderate or low aquatic affinity, whereas its body mass was estimated by Brocklehurst et al. (2022) at less than 1 kg. To incorporate this uncertainty into our parameter estimates, we specified six alternative models using MCMCglmm, with all possible combinations of (a) a low or moderate aquatic affinity, and (b) a body mass of 2, 500 or 1000 g, and combined their posterior distributions (Supplementary Section S3.4).

We included no explanatory variables in the models, other than a separate intercept per response variable, on which we specified a phylogenetic random effect to account for the evolutionary relationships across species. We summarized the posterior distributions of model parameters (e.g. correlations between response variables, thresholds) by calculating the median of each distribution and the 95% highest posterior density (HPD) interval. Given that body mass correlated strongly with metabolic rate, brain mass and maximum longevity, as expected, we removed the contribution of body mass from each of these three traits (Supplementary Section S3.5) and fitted the models again using the mass-corrected traits. Further details on the specification of these models are available in Supplementary Section S3.

2.4.3 | Comparison of torpor-capable species

To understand (a) whether daily heterotherms and hibernators differ systematically in their physiology and ecological preferences, and (b) whether there are multiple subtypes of daily torpor and hibernation, we compared torpor-capable species based on the 21 ecophysiological variables in our study. To this end, we first extracted the posterior distributions of the 21 variables per species from the MCMCglmm fits. For each posterior distribution, we compiled a table of the median and the bounds of the 95% HPD interval. By doing so, we were able to (a) include species with missing values in one or more variables (Supplementary Section S3.1) and (b) explicitly account for the uncertainty around each estimate, which may depend on the pattern of data missingness and the position of the species in the phylogeny. Next, we applied a phylogenetic principal components analysis (pPCA) to the aforementioned table, accounting for the strength of the phylogenetic signal in the data (the λ parameter), as implemented in the phytols R package.

We then examined how daily torpor and hibernation are distributed across the first four phylogenetic principal components. Furthermore, to identify torpor subtypes that are associated with distinct areas of the ecophysiological space (i.e. distinct niches), we applied Gaussian mixture model clustering to pPCA scores using the mclust R package (v. 6.0.0; Scrucca et al., 2016), setting the number of clusters between 1 and 5. The optimal mixture model was automatically determined using the Bayesian information criterion (Schwarz, 1978). We additionally examined the distribution of three torpor descriptors introduced by Nowack et al. (2023) across the first four phylogenetic principal components (Supplementary Section S6.1).

2.4.4 | Ancestral state reconstruction of torpor and robustness analysis

To infer whether hibernation was present in early ancestors of modern mammals and birds, we reconstructed the ancestral torpor states of major avian and mammalian clades according to both the Mk and MCMCglmm fits. For the latter model, we extracted the posterior torpor probabilities that were already calculated for all internal

nodes of the phylogeny during the fitting process. For the Mk model, we conducted 10,000 stochastic character mapping simulations (Bollback, 2006; Huelsenbeck et al., 2003) using the make.simmap function of the phytools R package. In these simulations, we set the transition rate matrix and the torpor probabilities at the root of the tree to the previously obtained model-averaged estimates.

Given that (a) placental mammals were the group with the highest number of torpor shifts in our dataset and (b) our knowledge of which species are capable of torpor remains incomplete, we further investigated the robustness of the torpor probabilities for the last common ancestor of modern placental mammals. To this end, we assumed that a certain number of placental mammals, currently not known to be torpor-capable, are in fact torpor-capable, and we randomly switched 20, 85 or 200 of them from no torpor to either daily torpor or hibernation. These correspond to 5.08%, 21.57% and 50.76% of the torpor-incapable placental mammals in our dataset. We performed this process five times, fitted the Mk and MCMCglmm models to all 15 resulting datasets and re-estimated the torpor probabilities of Placentalia as described earlier.

All computational analyses described in this study were executed on compute nodes equipped with AMD EPYC 7702 CPU cores for a cumulative runtime of ~101,600 CPU hours (see also Supplementary Section S3.4).

3 | RESULTS

3.1 | Evolutionary transitions among torpor states

To address whether daily torpor and hibernation are discrete torpor states or parts of an evolutionary continuum (Figure 1), we reconstructed the pattern of evolutionary transitions among these three states based on fits of the Mk model. We found strong support for frequent evolutionary transitions between no torpor and daily torpor, and between daily torpor and hibernation, but direct transitions between no torpor and hibernation were nearly nonexistent (Figure 2b). Considering the possibility that the few observed apparent direct transitions (Supplementary Section S1) may involve a transient and unobserved daily torpor state, this result provides strong support for the evolutionary continuum hypothesis. It also justifies our treatment of torpor as a threshold trait in our multi-response generalized linear mixed models. In these models, median estimates of torpor liability for the 1338 species covered nearly the entire continuum (Figure 2b,c). For example, liabilities of species capable of daily torpor ranged from relatively low (just above the no-torpor threshold) to intermediate to relatively high (just below the hibernation threshold).

3.2 | Associations of torpor with ecophysiological factors

We next examined the associations between torpor and the 21 ecophysiological variables that we collected. Across all 1338 extant

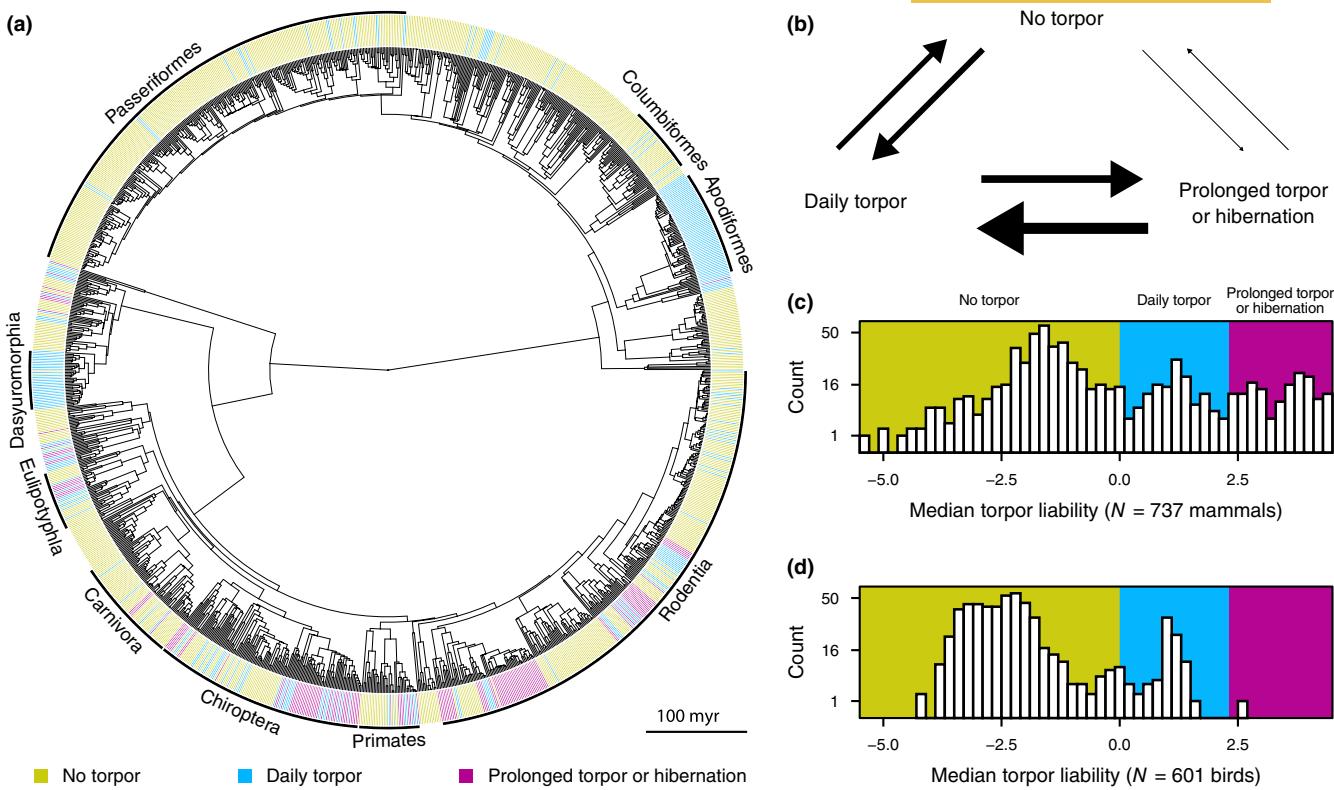


FIGURE 2 Distribution of torpor across the phylogeny of mammals and birds and evolutionary patterns thereof. (a) The most species-rich orders in our dataset are explicitly shown. (b) The pattern of evolutionary shifts among torpor states, as reconstructed with variants of the Mk model. (c, d) Median posterior torpor liabilities for all extant mammals (c) and birds (d) in our dataset, as estimated with MCMCglmm fits (see Section 2). Thresholds are denoted by a shift in background colour. Note that values along the vertical axes do not increase linearly so that both small and large counts are distinguishable.

mammalian and avian species in our dataset, we were able to detect systematic correlations with torpor (i.e. with a 95% HPD interval that does not include zero) for 16 of the 21 variables (Figure 3). For those, median posterior correlation estimates ranged from -0.33 to -0.13 (negative associations) and from 0.12 to 0.32 (positive associations). The variables that correlated most strongly and positively with the ability to enter torpor were temperature seasonality and absolute latitude at the middle of each species' range, nocturnality and carnivory. In contrast, torpor was most strongly negatively correlated with net primary productivity, annual precipitation and mean temperature at the range centre, as well as with body mass and cathemerality. All remaining variables (e.g. basal metabolic rate and fossoriality) correlated more weakly with torpor.

Next, we investigated associations between torpor and ecophysiological variables, separately for mammals and for birds. Including only mammals in the correlations analysis produced qualitatively identical results for most variables. Specifically, correlations obtained with the entire dataset generally increased in strength when only mammals were included. The main exception was the correlation with hemisphere which was marginally supported across the entire dataset (95% HPD interval=[0.002, 0.247]) and not supported for the mammalian subset (95% HPD interval=[-0.016, 0.278]). In contrast, including only birds in the analysis resulted in much weaker correlations with torpor for all 21 variables. In particular, the

correlation with body mass was the only systematic correlation for the avian subset of the data.

3.3 | Variation among torpor-capable species

A pPCA of the 21 ecophysiological variables across only torpor-capable species revealed extensive overlap between daily torpor and hibernation in the parameter space (Figure 4). Clustering of the resulting pPCA scores did not support the existence of multiple subtypes of daily torpor and hibernation, tied to specific physiological, ecological or climatic factors. Instead, variation among torpor-capable species was strongly taxonomically structured (Figure 5). Analysing mammals separately and examining the distribution of the three torpor descriptors of Nowack et al. (2023)—seasonality, predictability and preparation for hibernation—across the first four pPCA principal components led to similar conclusions (Supplementary Section S6).

3.4 | Origins of hibernation in mammals and birds

To address our third key question, we next inferred whether the early ancestors of mammals and early ancestors of birds were

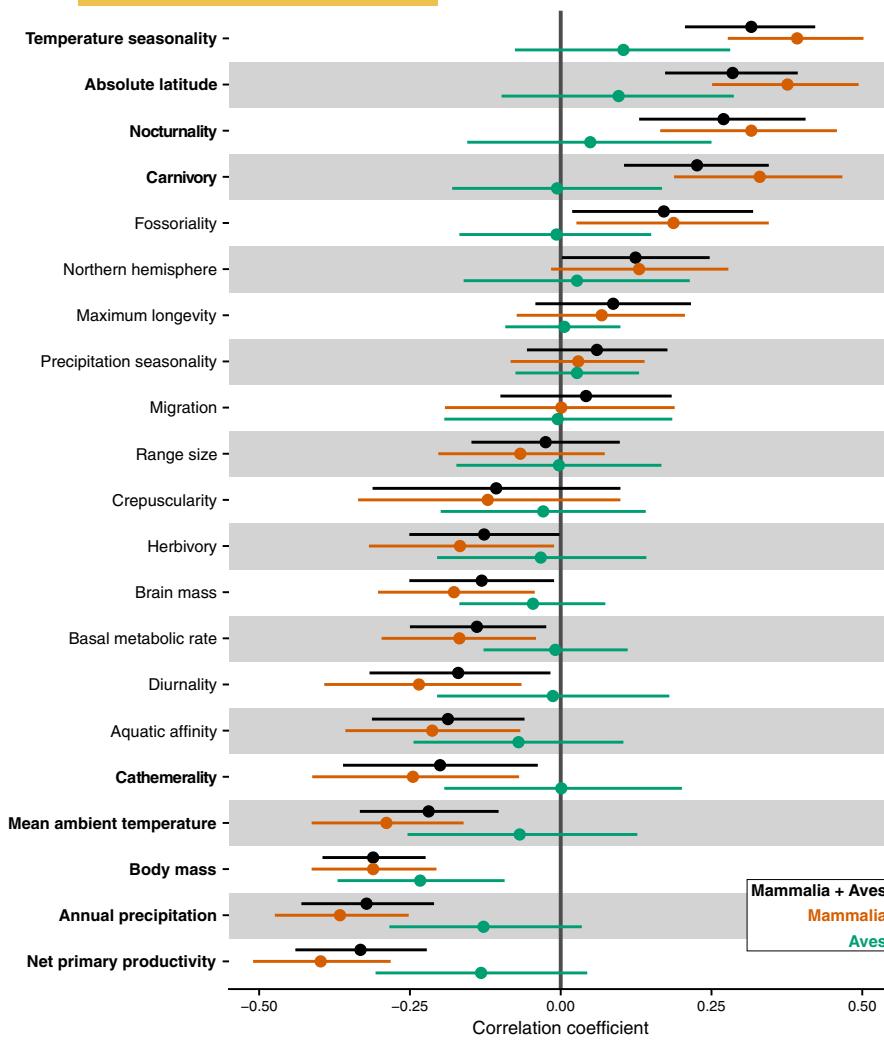


FIGURE 3 Correlations between torpor and ecophysiological variables. Circles stand for the median posterior estimate of each correlation coefficient, whereas horizontal lines represent its 95% HPD interval. Systematic correlations are considered as those with a 95% HPD interval that does not include zero. Variables shown in bold have an absolute median correlation estimate of at least 0.2 across the entire dataset (Mammalia + Aves). Basal metabolic rate, brain mass and maximum longevity were corrected for body mass (Supplementary Section S3.5).

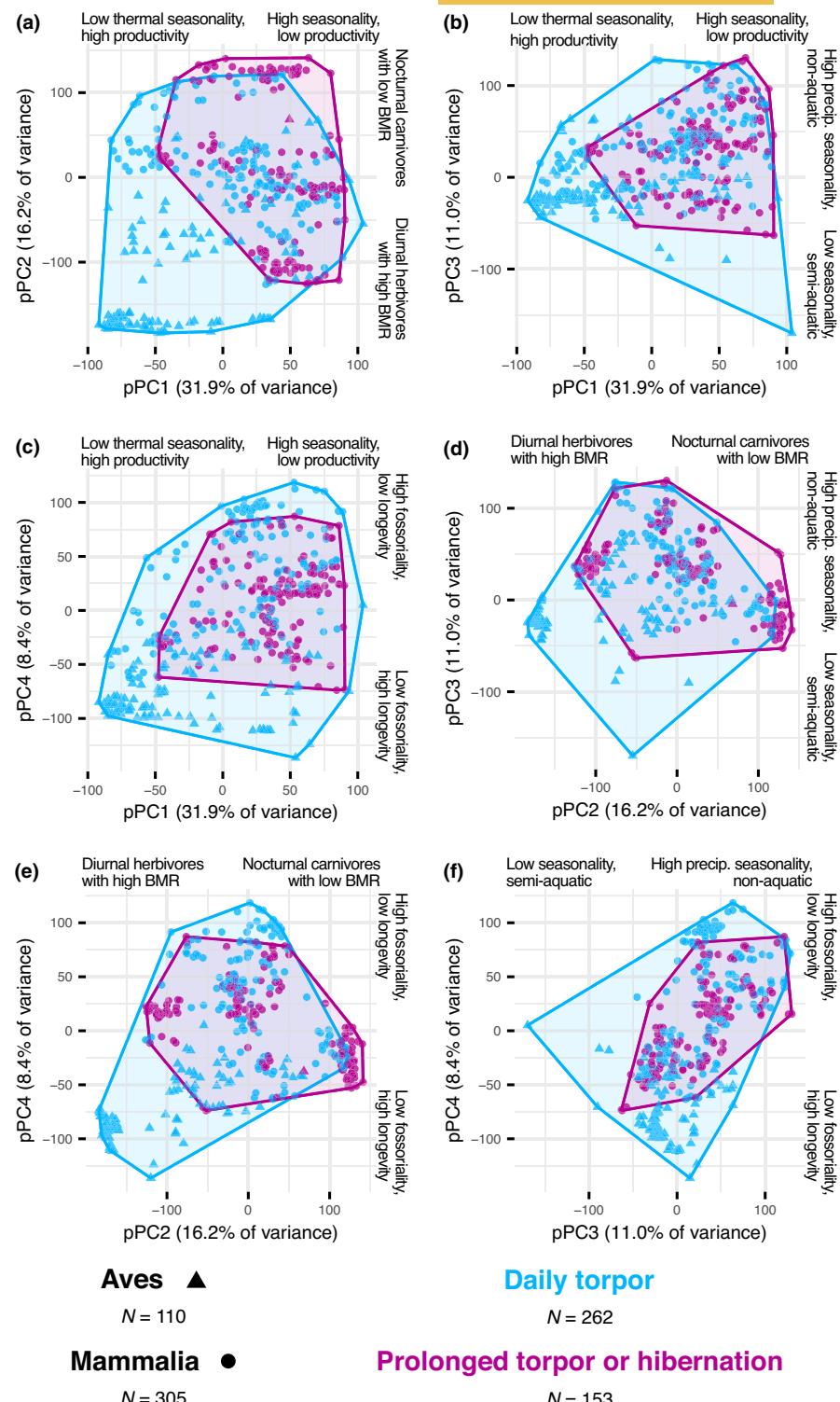
capable of hibernation. In all deep nodes that we examined, we estimated a low probability for hibernation, according to both Mk and MCMCglmm fits (Figure 6a,b). For the last common ancestor of extant placental mammals (LCAP), we additionally tested the robustness of this estimate to assuming that our knowledge of torpor-capable species is incomplete by randomly switching 20, 85 or 200 of the torpor-incapable placental mammals to either daily torpor or hibernation. This test showed that our finding of a low probability for hibernation for the LCAP was almost always robust (Figure 6c,d). We only obtained a high probability of hibernation for two of the five tests when switching the torpor capabilities of 200 species. However, in these two tests, the Mk model assigned a non-negligible weight to direct evolutionary transitions between no torpor and hibernation (Figure 6c,e). In other words, even after switching >50% of the torpor-incapable placental mammals, a high probability of hibernation in the LCAP is only possible if daily torpor and hibernation are discrete evolutionary states, which violates the strongly supported evolutionary torpor continuum hypothesis. This also explains why MCMCglmm fits—which necessarily impose a continuum in torpor—never estimated a high probability of hibernation in the LCAP, even when we modified the torpor capabilities of 200 species (Figure 6d).

4 | DISCUSSION

In this study, we compiled a comprehensive dataset of torpor capabilities of 1338 extant mammals and birds, along with 21 ecophysiological variables for each species and for a few ancestral taxa based on palaeobiological studies. By applying a series of phylogenetic comparative methods to the data, we addressed three key questions regarding the evolution of torpor as a key survival strategy for many mammals and birds.

Our first key question was whether daily torpor and hibernation are evolutionarily distinct states or if an evolutionary continuum exists from homeothermy through daily torpor to hibernation (Figure 1). Our results strongly support the evolutionary torpor continuum hypothesis, as (a) evolutionary transition rates were very high between daily torpor and hibernation, and extremely low between no torpor and hibernation (Figure 2b), and (b) daily heterotherms and hibernators overlapped remarkably in the ecophysiological space (Figure 4). Direct transitions between no torpor and hibernation were detected in only 11 out of 2625 branches of our phylogeny, distributed across various groups, including in the Sciuroomorpha, Arctoidea and Xenarthra (Supplementary Section S1). Some direct transitions may be artifactual, arising from errors in tree topology

FIGURE 4 (a-f) Projection of daily torpor (blue) and hibernation (purple) onto the first four principal components of a phylogenetic PCA of 21 ecophysiological variables for torpor-capable species only (see Section 2). For each principal component, the variables that most strongly correlate with it are explicitly listed.



or branch lengths, errors in torpor classification (e.g. a daily heterotherm being classified as incapable of torpor) or strong increases in the evolutionary rate of torpor in some lineages, possibly driven by adaptation to novel environments, that could have resulted in a transient but unobserved (given the available data) daily torpor state on the path to hibernation. Differentiating among these possible explanations for a given direct transition would require further fieldwork, experiments and computational investigation, and

can be the focus of future studies. An interesting example is the torpor-incapable white-tailed antelope squirrel (*Ammospermophilus leucurus*), which accounts for one of the three direct transitions between no torpor and hibernation (two in this direction and one in the opposite direction) in the Sciromorpha suborder (Supplementary Figure S1). *Ammospermophilus leucurus* is nested within a clade of 33 hibernators, but the species has been well-studied both in its natural environment and experimentally, and there is currently no

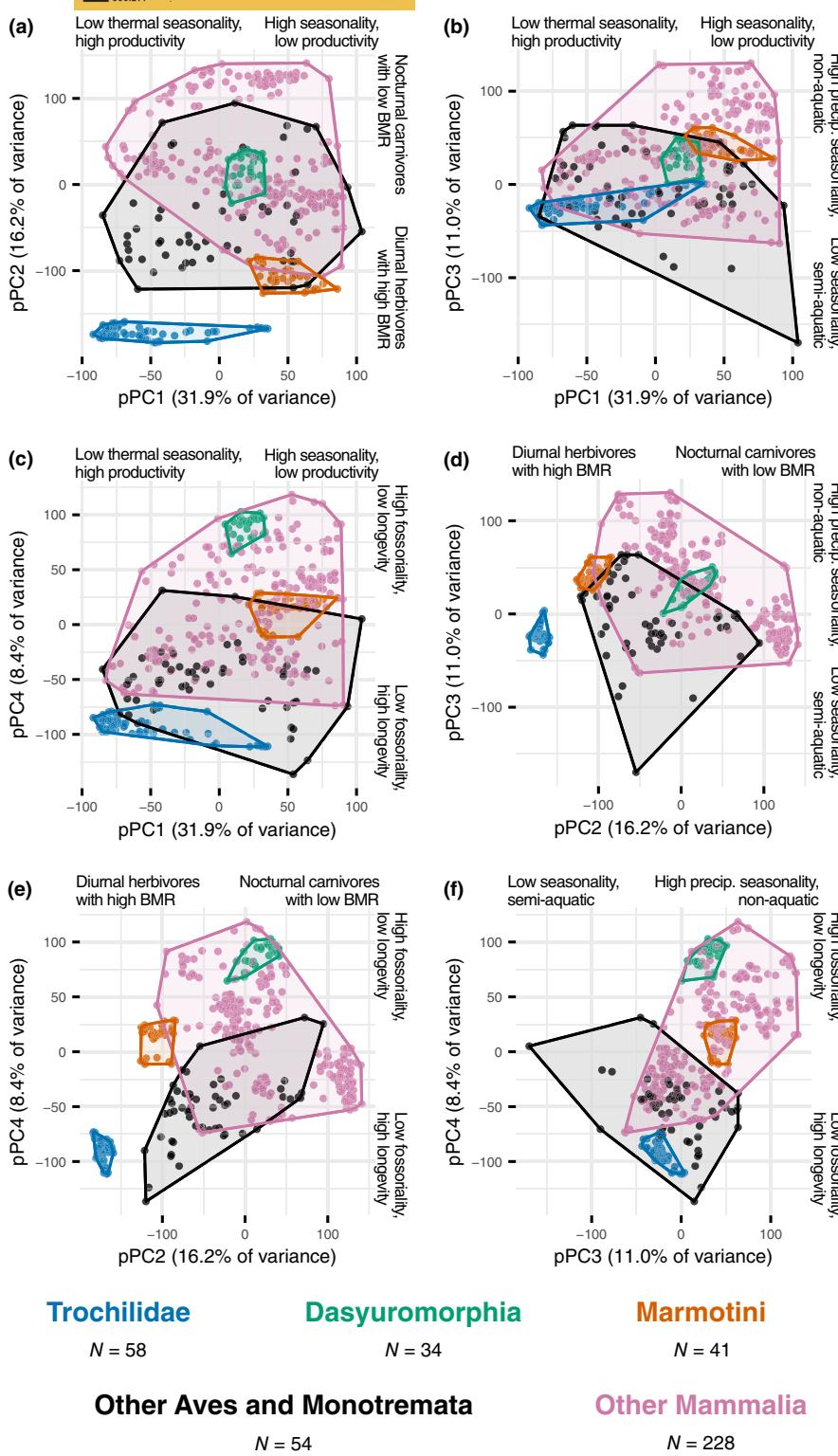


FIGURE 5 Clustering of torpor-capable species based on their distribution throughout the ecophysiological parameter space, as inferred from the phylogenetic PCA. Panels (a)–(f) show all pairwise combinations of the first four phylogenetic principal components. Note that three of the five clusters are monophyletic.

evidence that it can enter controlled torpor (Karasov, 1983; Refinetti & Kenagy, 2018, 2023). Thus, with very few possible exceptions, our analyses show that torpor largely evolves along a continuum.

The second question that we addressed was whether torpor in endotherms is strongly linked to specific ecophysiological factors, regardless of taxonomic group. To this end, we treated torpor as a threshold trait—justified by the aforementioned support for an evolutionary torpor continuum—and simultaneously estimated

the correlation structure among torpor and 21 ecophysiological variables, accounting for phylogeny. Across all endotherms in the present study, several variables correlated systematically with torpor (Figure 3). Specifically, we found that torpor is linked with living in a low-productivity environment with high thermal seasonality, nocturnal activity patterns, an at least partly carnivorous diet (including insectivory) and a small body mass. However, we should note that these correlations are overall weak, with median

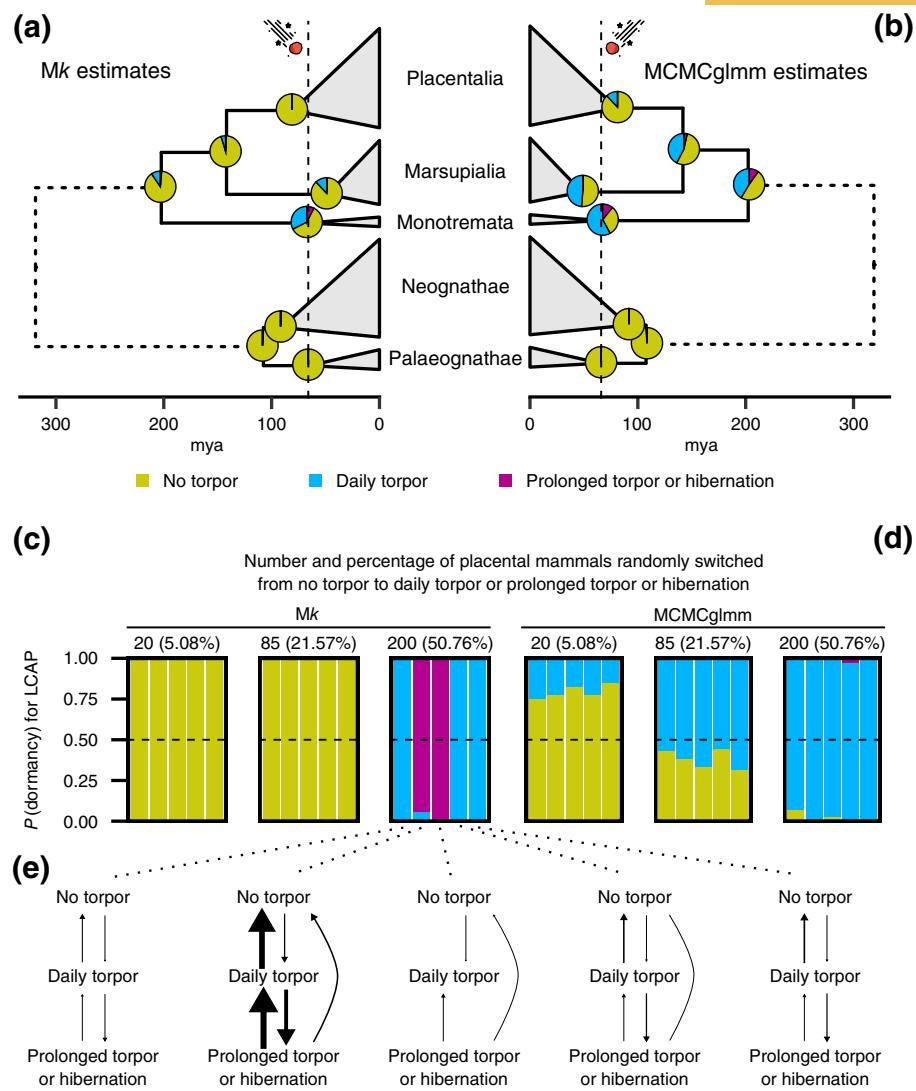


FIGURE 6 Ancestral state reconstruction of torpor for selected deep nodes of our phylogeny. (a, b) Torpor probabilities according to Mk and MCMCglmm fits. The dashed vertical line at 66 mya indicates the Cretaceous–Palaeogene boundary. (c, d) Probabilities of the three torpor states for the last common ancestor of Placentalia (LCAP), according to Mk and MCMCglmm fits after randomly switching 20, 85 or 200 torpor-incapable placental mammals to torpor-capable, replicated five times. (e) Reconstructed evolutionary transitions among torpor states, as inferred with variants of the Mk model, after switching 200 placental mammals from torpor-incapable to either daily torpor or hibernation.

posterior correlation estimates not being higher than 0.32 or lower than -0.33.

The detected associations between torpor and environmental conditions are in line with the expectation that torpor should be most beneficial in environments with seasonal variation in temperature and food availability, and less so in thermally stable, highly productive environments. Nevertheless, such associations may also partly reflect the fact that most research effort has been focused on species living in seasonal environments (Levesque et al., 2023; Nowack et al., 2020), possibly resulting in an underestimation of the torpor capabilities of species at low latitudes. Furthermore, particularly in the tropics, torpor expression could be constrained by high environmental temperatures which can mask the ability of species to use torpor (Levesque et al., 2014; Nowack et al., 2020).

Besides a possible bias towards seasonal environments, most previous studies on torpor have also predominantly focused on species from the northern hemisphere (Nowack et al., 2020). This may explain the positive (albeit weak and marginally supported) correlation between torpor and the northern hemisphere (Figure 3). In any case, as Nowack et al. (2023) showed, there are differences in torpor use, type and seasonality between the Holarctic region of the northern hemisphere and the rest of the world.

Our finding of a link between torpor and nocturnal activity patterns is consistent with nocturnality being more energetically demanding than diurnality, given that nocturnal species are active under lower ambient temperatures than their diurnal counterparts (Levy et al., 2012; van der Vinne et al., 2015, 2019). When energetically challenged, some nocturnal species tend to shift to diurnality (e.g.

see Hut et al., 2012; van der Vinne et al., 2019; Weyer et al., 2020) and, therefore, undergoing torpor would be another highly beneficial strategy. Nocturnal species also have the advantage of being able to rearm passively with rising ambient temperatures which lessens the costs of rewarming from torpor (Lovegrove et al., 1999).

The positive association between torpor and carnivory (including insectivory) is likely also driven in part by climate, given that the abundances of many insect species—that serve as prey for insectivorous endotherms—can strongly vary over time, as a function of factors, such as temperature and precipitation (e.g. see Bowles et al., 2002; Guédot et al., 2018; Kishimoto-Yamada & Itioka, 2015). Thus, for insectivorous hibernators (e.g. tenrecs, hedgehogs, bats), timing hibernation to coincide with periods of low insect abundances would confer significant energy savings (Humphries et al., 2003; Meyer et al., 2016). Other carnivorous diets may also be linked to torpor in different ways. For example, brush-tailed mulgaras (*Dasyurus blythii*) with a higher proportion of vertebrates in their diet were found to enter torpor less frequently and for shorter periods (Pavey et al., 2009), likely due to the higher average energy content of vertebrates compared with those of invertebrates or plants. Therefore, future studies could compare the impacts of various carnivorous diets on the torpor characteristics of diverse species. It is also possible that (a) the different macronutrient compositions of carnivorous and herbivorous diets and (b) potential differences in the thermal tolerance of the gut microbiomes of carnivorous and herbivorous species (Fontaine & Kohl, 2023; Hardison & Eliason, 2024) may play additional roles in the evolution of torpor, but research on these topics is lacking.

At the physiological level, a negative correlation of torpor with body mass partly represents a biophysical constraint, given that the maximum rates of cooling and rewarming are inversely proportional to body mass (Geiser, 2021; Geiser & Baudinette, 1990; McKechnie & Wolf, 2004). This suggests that above a certain body mass threshold, the energy expenditure at the beginning and end of torpor would exceed the amount of energy conserved during torpor, making it an unfavourable strategy. A key exception to this torpor-size 'rule' are hibernating bears. While their metabolic rate is greatly reduced during hibernation, their body temperature falls to only around 30°C (Evans et al., 2016; Hissa, 1997; Tøien et al., 2011), in contrast to smaller hibernators, such as the Arctic ground squirrel (*Urocitellus parryii*) and the hazel dormouse (*Muscardinus avellanarius*) whose body temperatures can become as low as -2.9°C (Barnes, 1989; Pretzlauff & Dausmann, 2012). This allows bears to enter and exit torpor relatively quickly, enabling hibernation despite their high body mass.

Including only mammals in the analysis of torpor correlations yielded similar results, with most correlations increasing in strength, whereas, across birds, the only systematic correlation for torpor was a weak negative correlation with body mass. The absence of multiple systematic correlations in birds may be explained by multiple factors. First, compared with mammals, birds have a much sparser distribution of torpor which—with the exception of hummingbirds—tends to be more scattered across avian clades (Figure 2a). This would

necessarily lower the signal-to-noise ratio across birds compared with mammals, hindering the detection of systematic associations. Second, the increased mobility of flying species, which facilitates migration likely contributes to the apparent decoupling of torpor from environmental variables in birds. Many birds employ seasonal migration to avoid adverse environmental conditions, a strategy that is sometimes combined with torpor to reduce energy expenditure at stopovers, decreasing the time required for refuelling (Carpenter & Hixon, 1988; Clerc & McGuire, 2021; Eberts et al., 2021; McGuire et al., 2023; Wojciechowski & Pinshow, 2009). It is also worth pointing out that the common poorwill (*Phalaenoptilus nuttallii*), the only bird known to hibernate, also migrates in a seasonal manner (Csada & Brigham, 1994; Woods & Brigham, 2004). Such behaviours would explain why the climatic conditions at the centre of the range are poor predictors of the torpor capabilities of bird species. In contrast, across mammals, climatic variables exhibit much higher predictive power for torpor, given that long-distance migration is mainly limited to large-bodied species (that are typically torpor-incapable) and bats (in which torpor-assisted migration has been observed; Supplementary Figure S12; Baloun & Guglielmo, 2019; McGuire et al., 2014, 2023; Webber & McGuire, 2022).

Our last key question was whether the early ancestors of modern endotherms were capable of hibernation which was later lost by most lineages, or whether multiple lineages evolved hibernation independently. Our results support the latter scenario given that, for the deepest nodes in our phylogeny, hibernation was the least likely state according to both Mk and MCMCglmm fits (Figure 6a,b). Interestingly, this includes nodes both before and after the Cretaceous–Palaeogene boundary, suggesting that hibernation may not have been a key ability for the survival of certain endothermic lineages during that mass extinction event. Daily torpor, on the contrary, is likely to have been practised by some early mammalian ancestors, including that of the Monotremata and that of the Marsupialia. This type of torpor would also allow for a reduction in energy expenditure (albeit less pronounced than that achieved through hibernation) under challenging environmental conditions. Overall, our results suggest that early mammalian and avian ancestors did not hibernate, with this trait emerging independently from daily torpor in many lineages of endotherms, enabling them to occupy a wide diversity of niches.

A scenario of repeated independent gains (and losses) of hibernation and daily torpor may appear counterintuitive given the complex physiological processes that are responsible for entering, maintaining and exiting torpor (e.g. see Fu et al., 2020; Junkins et al., 2022; Mohr et al., 2020). Nevertheless, it can explain the remarkable variation in the physiologies, ecological strategies and torpor characteristics present among torpor-capable endotherms (Figures 3–5; Supplementary Figures S13–S16; Geiser, 2021). Such a scenario is also consistent with the reconstructed evolutionary transitions among torpor states (Figure 2b), given that shifts (a) from no torpor to daily torpor and (b) from daily torpor to hibernation are relatively frequent, whereas shifts between no torpor and hibernation are almost nonexistent. It is also worth mentioning that many other complex traits have evolved convergently multiple times, including vision (Nilsson, 2021), flight

(Alexander, 2015), extreme longevity (Yu et al., 2021) and the return to a fully aquatic lifestyle (Houssaye & Fish, 2016).

A limitation of our study is that although we included some palaeobiological data in our analyses (Supplementary Section S2.2), all our torpor classifications come from extant species. This reflects the inherent difficulty in accurately characterizing the torpor capabilities of mammalian and avian fossils. A notable exception is a study by Whitney and Sidor (2020), which presented evidence for torpor in the tusks of fossil specimens of the non-mammalian synapsid *Lystrosaurus*. This taxon comes from a sister lineage to all extant mammals, with the last common ancestor of these lineages ('Therapsida') occurring ~275 million years ago (Lungmus & Angielczyk, 2019). Because of this large evolutionary distance, *Lystrosaurus* would not be very informative for our analyses, given that evolutionary shifts in torpor use can occur within only a few million years (see Supplementary Section S1.1). For this reason, we chose not to include this taxon in our dataset. It is worth noting that despite the existence of torpor-capable species among monotremes and marsupials, the last common ancestor of Placentalia was reconstructed with a very low probability of torpor (Figure 6a,b). This highlights the weak influence of distantly related taxa on the estimated torpor capabilities of key ancestors of extant endotherms. Nevertheless, future palaeobiological studies could further explore the pattern of torpor occurrence among mammalian and avian fossils when more relevant data become available.

In conclusion, our study shows that daily torpor and hibernation are not evolutionarily distinct torpor states and that torpor likely emerged independently multiple times across endotherms and in different ways. As a result, knowledge of the patterns and molecular underpinnings of torpor of a given species may not be directly transferable to other, evolutionarily distant species, even if they occupy similar niches. Thus, more attention should be paid to thoroughly characterizing the torpor capabilities and patterns—at the molecular, physiological or ecological level—of species representing diverse clades. This will both deepen our understanding of the similarities and differences in torpor across narrow and broad taxonomic groups, and improve our ability to forecast the responses of torpor-capable endotherms to future environmental challenges.

AUTHOR CONTRIBUTIONS

Dimitrios-Georgios Kontopoulos and Michael Hiller conceived the study and designed its methodology. Dimitrios-Georgios Kontopoulos and Danielle L. Levesque compiled the data. Dimitrios-Georgios Kontopoulos analysed the data, generated figures and led the writing of the manuscript. Michael Hiller provided access to computational resources and supervised the study. All authors contributed critically to the drafts and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

Danielle L. Levesque is an associate editor of *Functional Ecology* but was not involved in the editorial handling of this manuscript.

DATA AVAILABILITY STATEMENT

All data collected for this study, as well as the phylogeny that was used, are available from Figshare at <https://doi.org/10.6084/m9.figshare.24746283> (Kontopoulos et al., 2024a). The source code for the analyses of this study is available from GitHub at https://github.com/dgkontopoulos/Kontopoulos_et_al_torpor_evolution_2025 and archived on Zenodo at <https://doi.org/10.5281/zenodo.14385989> (Kontopoulos et al., 2024b).

STATEMENT ON INCLUSION

This study brings together authors from different nationalities (Greek, Canadian and German), scientific backgrounds and career stages, which led to frequent and fruitful exchanges of diverse perspectives. Our analyses relied on a plethora of previously published global datasets and did not require additional fieldwork or experiments.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Appendix S1: Direct shifts between no torpor and hibernation according to the Mk model.

Appendix S2: Ecophysiological data used in this study.

Appendix S3: Additional MCMCglmm specification details.

Appendix S4: Comparisons of the predictions of MCMCglmm fits with data.

Appendix S5: The relationship between migration and body mass in endotherms.

Appendix S6: Further analyses of the distribution of torpor along the ecophysiological parameter space.

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